XYLOTOMY OF CYCADALES AND THE STRUCTURE OF THE LEAF EPIDERMIS*

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Cycadales are likely to have been spread all over the Earth already late in the Palaeozoic and particularly in the Mesozoic. At present they exist in no more than 10 genera and about 75 species exclusively in tropical and subtropical regions. Some of these genera are found in America only *(Dioon, Zamia, Ceratozamia, Microcycas)*, others in Africa *(Encephalartos, Stangeria)* or in Australia *(Macrozamia, Lepidozamia, Bowenia)* and it is but the *Cycas* genus in the strict sense of the term that spreads all over the vast area from Madagascar over India and Southern China to Japan and the Polynesian Archipelago. Not a single species represents *Cycadales* in Europe. This high degree of dispersion reflects their considerable geological age.

Due partly to this high degree of dispersion it is rather cumbersome and difficult, in some cases even impossible to obtain material for xylotomic examination. This is why comparatively few research workers were engaged in xylotomy of recent *Cycadales* up to now and no comprehensive work exists yet offering a complete elaboration of all genera of *Cycadales* living in our days. These considerations prompted the author to compose a xylotomical monograph on *Cycadales* as a continuation of his monograph on the Xylotomy of Conifers, following the same pattern. To construct this work — which is under way now — was desirable and necessary also to supply efficient aid to palaeontologists in determination of various stem relicts of *Cycadales*. The present study is a small selection from that work. To begin with, an attempt of general characterization of *Cycadales* is made, followed by the particular, individual, detiled xylotomy of two out of the about 40 species dealt with, and finally the structure of the epidermis of leaves of the same two species is discussed, since palaeontologists often endeavour to determine rests of *Cycadales* from the epidermis structures.

A short general xylotomical outline of recent Cycadales

The order of *Cycadales* living in our days comprises 9 or 10 genera respectively, namely: 1. *Bowenia*, 2. *Ceratozamia*, 3. *Cycas*, 4. *Dioon*, 5. *Encephalartos*, 6. *Lepidozamia*, 7. *Macrozamia*, 8. *Microcycas*, 9. *Stangeria*, and 10. *Zamia*. According to JOHNSON these 10 genera can be grouped in three families viz. I. *Cycadaceae*, II. *Stangeriaceae*, III. *Zamiaceae*. Although these 10 genera in their visible characteristics, in blossom formation, foliage etc. substantially differ from each other, nevertheless the stems exhibit characteristic features proper to all genera which are thus essentially different from all other woody plants, in the first place from Conifers in the strict sense of the word.

* A selection from a monograph soon to appear under this title.

Cross section. All genera and all species of *Cycadales* when examined in cross section display the very characteristic feature to contain a central core or pith, which is well differentiated and consists mainly of parenchyma cells (Fig. 1 *a*). The pith is profusely permeated by mucilage canals lined with epithelial cells (Plate I. Fig. 3). These canals generally communicate with the similar mucilage canals of the cortex through the primary pith rays. In the pith of most *Cycadales* among the so called own vascular bundles there are common bundles leading from the pith through the broader primary pith rays into the cortex and from there proceeding as true leaf trace bundles into the leaves (Plate II, Fig. 5). The collateral vascular bundles of the pith very often both in the pith and in the cortex are winding irregularly upside down, running at some places parallel to the axis, then again almost perpendicularly.

Another characteristic of *Cycadales* is that the well differentiated and developed pith is surrounded by 1—2—3-fold or multiple xylem and phloem rings or collateral vascular bundle rings respectively (Plate I, Fig. 1). Only in *Dioon spinolosum* is a well developed xylem and a much lesser phloem observed not followed by further phloem and xylem layers. In the xylem tracheids are arranged in most cases — similarly to the wood of Conifers — radially and in ± equal cross sections, but no annual rings can be distinguished in the xylem, because no such exist (Plate I, Fig. 9.). Pith rays are but exceptionally uniseriate, in most cases 2—10 and even 15-seriate (Plate II. Fig. 5.). These latter are the so called primary pith rays (Plate II. Fig. 5.) which run immediately from the pith towards the cortex. This multiseriate pith ray structure is a distinct *Cycadaceae* character as against the structure of the xylem in all Conifers. Therefore it is, in the author's opinion, — erroneous to determine a fossil containing multiseriate pith rays as Araucarioxylon. All walls of the pith ray cells are smooth and very thin; simple pits can be observed but in very exceptional cases.

The xylem ring is always enclosed by a phloem ring (Plate I. 4 *d*) and 1—2-seriate cambium may be inserted. In many cases the rather well differentiated collateral open bundles are arranged in a ring shape (Plate I., 1. *c, d*) and fascicular cambium can be observed among them. Sometimes phloem parenchyma and bast fibres as well as sieve tubes with tiny pores are included in the phloem, in a most specific and characteristic arrangement (Plate I. 5. 6.). Among the phloem elements, but — especially next to the xylem — also in the broader pith rays, idioblasts or transfusion cells frequently occur (Plate II. Fig. 1—4.), with various kinds of reticular thickening, the tracheids showing in their finer structure characteristic bordered or scalariform pitted thickenings. In some cases it is easy to observe that these transfusion cells are really ± isodiametrical protoxylem elements where the bordered or reticulate pits even in a very elongated form can still be recognized. These protoxylem cells more and more stretch towards the xylem, transforming into short tracheids and finally elongating as to become long tracheids. The elongation process of the tracheids can be closely followed in some cases as they are transforming from protoxylem elements.

Among the parenchyma cells of the cortex many mucilaginous ducts with large cavities are scattered while the xylem is covered from outsiede by flattened and suberized cortex cells (Periderm. See Photo). In the cortex cells and in the parenchyma cells beneath, calcium oxalate crystal druses rather frequently occur (See Photo).

In fossil stems, particularly in those from the Carbon, Perm, Trias and Jura, other cross section structures, different from this *Cycas* type may be found, e. g. in *Pteridospermae, Medullosae* etc. which are generally polystelic, the structure of the steles, however, by and large corresponding with that of *Cycadales.*

Tangential structure. The pith rays both in the xylem and phloem are of various height and width, definitely differing also in this respect from those of Conifers. Besides the few 1—2-seriate, there occur pith rays 5—6—10—15-seriate in width and 70—100-seriate in height. This multiseriate pith ray structure is a definite *Cycas* feature. On the tangential sections and microsections among the tracheids often enough very thin walled parenchyma cells are found (Plate II, Fig. 5. 7. 8. 9.).

Radial sections and microsections also exhibit many characteristic features, the most important being that the pith ray cells are nearly always in an erect position and in the cross-fields the several pits or pit rows are arranged not horizontally but vertically, in most cases according to the araucaroid pattern (Plate III, Fig. 1. 2. 3.). The pit aperture is as a rule horizontal or somewhat oblique. In genera which have scalariform pitted tracheids only, e. g. in *Zamia* or *Microcycas,* there are no definite cross-fields. In these cases even in the pith ray cells no pits are translucent or at least no such can be detected even by most careful observation (Plate III, Fig. 8.). When both kinds of pit occur, cross-fields or pits respectively can be only found where the tracheid with bordered pits meets smoothwalled pith ray cells.

In cross-fields standing mostly erect, the pits can be as many as 3 to 30 (Plate III, Fig. 7.).

An other characteristic of the family is that the tracheids are pitted. Some of the tracheids, e. g. in *Encephalartos,* have only pits of the araucaroid type (Plate III, Fig. 1. 2. 3.) while in other cases the tracheids are scalariform pitted according to the fern type (Plate III, Fig. 5. 6.); again in other cases the most various transitions of the bordered pits can be observed, including reticular thickening (Plate III, Fig. 9.). In some species spiral and ring shaped thickening is found (Plate III, Fig. 4.). The tracheids next to the phloem are generally araucaroid-pitted, whereas towards the protoxylem reticulate and subsequently scalariform-pitted, while the protoxylem elements are often enough thickened spirally or in ring shape (Plate III, Fig. 4.), being highly suggestive in such places of similar thickenings in the vessels of *Monocotyledons,* e. g. of Palms.

Let us examine, after this general characterization, two *Cycas* genera or species respectively, namely the monotypic *Microcycas calocoma* and the *Lepidozamia hopei.*

1. **Microcycas calocoma** (Miq.) A. Dc.

A monotypic species occurring in the higher mountains of Western Cuba and reaching sometimes a height of 10 to 12 m, in most cases however remaining much lower. No branching takes place as a rule though dichotomous branching is observed occasionally. The surface of the stem is more or less smooth, cicatrices leaving, however, a conspicuous mark. At the stem apex a crown of leaves is found; leaves about 60 to 100 cm large and paripinnate; 50 to 80 pairs of leaflets are on the leaf spine. The strobile is 50 to 70 cm long and 13 to 16 cm thick.

Habitus picture. I obtained the material for investigation from Ponce de Leon (Habana) to whom I wish to express my gratitude. The piece of stem was a disc of 10 cm in diameter and 2 cm in thickness (See Fig. 1). The desiccated material first of all has been put in water to swell. In two days the whole surface was covered by a mucilaginous substance. When the surface has been cleaned the macroscopic structure was easy to distinguish.

In the centre of the 10 cm stem the diameter of the extensive pith was about 2,5 to 3 cm. In the pith the mucilage canals were marked by light coloured points. After the pith follows the 1 cm broad ring of vascular bundles. It was visible with the unaided eye that the xylem was somewhat thicker than the phloem layer. There is only one such ring of vascular bundles, involving monoxylic type. Outside the single ring of vascular bundles there is a 2 to 2,5 cm thick cortex the structure of which is similar to that of the pith but for the periderm of a somewhat more compact consistence separates in the peripherical region. Examination of the sections made from the disc revealed more subtle details.

Cross section.

The pith. The pith consists of more or less thin walled isodiametric parenchyma cells which closely fit to each other, with intercellular ducts running at some places. The dimension of the parenchyma cells is 150 to 200 μ. In their thin wall here and there very tiny pits assemble in groups (Plate IV. Fig. 2. 3.).

Pith bundles. Among the parenchyma cells of the ground tissue are arranged the vascular bundles of the pith which mostly contain 8 to 10 to 20

loosely arranged tracheids including rare, very thinwalled and 1—2 thick-walled bast fibres. These bundles may well be the vascular bundles proper to the wood, but it is not impossible that they are common bundles and as such make their way through the primary pith rays into the cortex and further as leaf trace bundles into the leaves.

Mucilage canals. These canals which are lined with thin walled epithelial cells, also proceed or wind in the pith. Their diameter is 220 to 240 μ (Plate IV. Fig. 3 *a*).

Transfusion cells. These cells assemble in groups or rather aline behind each other in strings (Plate IV. Fig. 3, at the letter *b*). Some of the transfusion cells are isodiametric while others more stretched or elongated to become real tracheids. The cell walls are reticulated and scalariform pitted, a structure that can be traced back at places to bordered thickenings. Cell length ranges between 100 and 250 μ, with some much longer occurring too. Here and there they almost stick to the tracheid bundles, suggesting the tracheids to originate from the elongations of these transfusion cells (Plate IV. Fig. 6. 7. at the letter *b*).

Vascular bundle ring. (Plate IV. Fig. 2). The simple vascular bundle ring (monoxylic type) is found in the periphery of the pith. At places the wood ring is distinctly seen to consist of several smaller and broader or thinner bundles with the 2 to 10-seriate primary pith rays running among them (Plate IV. Fig. 2. 4. 5. *c, d*).

Pith rays. Structure and form of the primary pith rays are in complete accordance with those of the pith parenchyma cells. The definite absence of morphological distinctive marks gives a clear idea of the primary pith rays originating from the pith.

Vascular bundles. Xylem bundles. In the xylem bundles the tracheid rows are either single or 2—3—8 tracheid rows are fitted to each other thus forming a broader and continuous xylem bundle (Plate IV. Fig. 2.). Cross sections of tracheids represent quadrangles, pentagons or irregular polygons of varying shape and size. Their radial dimension is 40 to 70 μ, the width about the same. Here and there very thin walled parenchyma cells are found among them which contacting each other are in connection with the pith ray cells from which they as to shape and structure can be hardly distinguished (Plate IV. Fig. 5.).

Phloem bundles. The xylem ring is followed by a 2—3-seriate cambium zone with cells somewhat smaller than the pith ray cells and radially slightly flattened. The primary broader, but also the thinner pith rays continue to run through this zone into the phloem (Plate IV. Fig. 2.). Similarly, the phloem bundles continue to run in the width of the xylem bundles, thus the former are of the same width than the corresponding xylem bundles (Plate IV. Fig. 4.). In the phloem the thick — walled bark elements form major or minor groups, sometimes tangential lamellae, while in other cases they are scattered. Beside the bark elements here and there perforated transversal sieve-tube elements can be observed. The pores of the sieve-tubes are minute.

The cortex. Outwards the phloem ring is followed by the cortex layer, the thin-walled parenchyma cells of which have exactly the same structure as is found in the pith. Also in this layer there are mucilage canals (*e*) the structure of which is the same as in those of the pith, verifying the statement that they are through the primary pith rays in connection with the analogous ducts of the pith. Also the common vascular bundles run here which had penetrated from the pith through the pith rays into the cortex. Their structure corresponds to that of the former (Plate IV. Fig, 1. 3. *e*).

Periderm. The periderm extends in the external layer of the bark. Its phelloid cells with thin, suberized walls fit to each other in radial rows in a brick pattern. In some periderm cells calcium oxalate crystals are found, generally in broader or thinner layers. Crystallization took place probably in regular or rhombic system. They are mostly single, but in some cases form smaller groups of two or three; very exceptionally crystal druses are formed (Plate IV. Fig. 1. 3. *f*).

Tangential section. Pith rays. The sections made through the phloem bundle reveal the structure of the rays which are 1—10—12-seriate. The height of the pith ray cells at the tangential side is 180 to 200 μ, their width 70 to 80 μ. In some pith ray cells tiny calcium oxalate crystal druses are found (Plate V. Fig. 8.).

Vascular bundles. The fibres of the elongated phloem bundles are thick-walled, their cavities thin, fissure shaped. Also the tracheids of the xylem bundles are elongated, their walls generally show scalariform thickening (Fig. 8.).

Transfusion cells. In the tangential section transfusion cells, situated between phloem and xylem bundles, are particularly frequent. Their walls present scalariform and reticular thickening (Plate IV. Fig. 8. to the right).

Radial section.

Pith rays. In this section the radial sides of the broad pith rays are very conspicuous. The walls of the pith ray cells — at least of the inner pith ray cells — are quite smooth, while the walls adjoining the tracheids show larger or smaller simple pits in irregular arrangement. These pits, however, are not in accordance with those of the generally known cross-fields, since they do not correspond to the pits of the tracheids behind them. This arrangement of the pits in the pith ray cells definitely differs from that in all other Conifers by not having borders at all, since such are only formed in the primary wall. The height of the pith ray cells at this side is 150 to 200 μ and they are rather erect quadrangles rounded off which in succession closely fit to each other. Thus there is no cross-field in the *Microcycas* (Plate IV. Fig. 9.).

Longitudinal tracheids. The tracheids are pitted in a rather diversified way. In the walls of some tracheids there are bordered pits only while in others the thickening is scalariform or reticulate. These tracheids with varied pits are arranged sometimes close to each other while in other cases only scalariform tracheids are found in some places (Fig. 10.) and only spiral tracheids in others. Some tracheids occasionally touch each other at the ends with transversal

walls, these being pitted similarly as the longitudinal walls. The bordered pits, however, fit to each other on the radial wall invariably according to the araucaroid pattern (Fig. 11. 12.).

The structure of the epidermis of leaves in Microcycas calocoma

A hypostomatic leaf with no stomata on the upper surface of the leaf blade, while on the lower surface the stomatal apertures are arranged in strips, each strip containing 4 to 6 rows of stomata successively, although this is no general rule. On the upper surface the epidermis cells are considerably elongated, their length ranging between 100 and 200 μ, their width between 20 and 25 μ. They are fitted to each other by longitudinal oblique walls, in other cases with transversal end walls. The walls are as a rule smooth or slightly undulating. The stomata are flanked by complementary cells. The dimensions of the stomata, guard cells included, are 65 to 70 μ, their width 35 to 40 μ. The width of the upper aperture is 22 μ, its length 20 to 21 μ. Thus the aperture is more of a lying ellipse, slightly tapering towards the small axis. Similarly tapering are the two ends of the guard cells. On the lower surface the epidermis cells are comparatively much shorter than within the strips or on the upper surface of the leaf (Plate VIII. *a*. Fig. 1—4.).

2. **Lepidozamia hopei** REGEL.

SCHUSTER in his monograph on *Cycadaceae* describes this species as *Macrozamia Denisonii* var. *hopei* (HILL) SCHUSTER, while JOHNSON in his recent work confers to it not only specific but generic rank, replacing it in the *Lepidozamia* genus established by REGEL in 1857.

The *Lepidozamia* genus comprises at present two species: *Lepidozamia hopei* REGEL occurring in a narrow area of the northeastern corner of Australia and *Lepidozamia peroffskyna* which is found exclusively in a narrow eastern coastal sector of Australia (see map). By the courtesy of Mr JOHNSON I succeeded in obtaining from the Brisbane Botanic Garden (Forestry Department) a desiccated *Macrozamia hopei* stem piece the size of which was about 30 cm, diameter 12 cm (see Photo). The marks of the cicatrices were already completely vanished from the exterior of the stem piece the yellowishbrown surface of which thus became completely smooth.

The stem of *Lepidozamia* may reach a height of even 20 m. on the apex the 2 to 3 m long leaves are grouped in a leaf crown. On some leaves as many as 160 to 200 pairs of leaflets may be found. The strobile can have a length of 40 to 60 cm and a diameter of 20 to 25 cm.

Habitus picture. From the desiccated stem piece a thin disc has been cut, softened in water and the surface subsequently cleaned. This surface is represented in Fig. 1.

The polyxilic structure of the stem could be immediately ascertained on the cross section picture. The diameter of the extensive dark coloured pith was 6,5 cm (*a*). In the interior of the pith in the ground tissue the proper and

common vascular bundles and the mucilage canals were scattered. These are indicated on Fig. 1. by the dark points. After the pith followed the vascular bundle ring, that is the first, so called normal vascular bundle ring (*c, d*), the xylem of which was 7 mm thick while the phloem 3 mm. The first abnormal xylem ring was somewhat thinner (4 mm) while the phloem ring measured hardly 2,5 mm. These data are in complete agreement with the statement of WORSDELL who dealt with the anatomy of *Lepidozamia peroffskyana* some 70 years ago. The double vascular bundle ring is followed by the narrow cortex (*e*) and by the periderm, the thickness of which is hardly 1 to 2 mm (*d*). (Plate VI. Fig. 1—2.).

Cross section. The pith is filled out with more or less isodiametric, thin-walled, loose parenchyma cells (Fig. 5.). In the cells there is a rich content of starch granules. These are markedly large (35 to 40 μ), somewhat excentric and often the starch is semi-conjugate. The walls of the parenchyma cells are very thin, even simple pits can be hardly observed. Among the cells of the thin-walled ground tissue at places idioblasts with thicker walls are found (Fig. 6.). In the pith the vascular bundles are winding to and fro, lending themselves very rarely to the production of a regular cross section picture; similarly, from the longitudinal sections only very small portions can be prepared (Fig. 2.). In the vascular bundles of the pith 35 to 40 tracheids are found in the xylem while the phloem is much less and hardly conspicuous. Sporadically some of the parenchyma cells are filled with calcium oxalate crystal druses, of which sometimes two are found in a cell. Next to the bundles mostly mucilage canals are running (Fig. 3. 5.). In the periphery of the pith where the vascular bundles begin, no transfusion cells, mentioned by WORSDELL in his study, were found; at most some thick-walled idioblasts were observed at the endings of the xylem bundles. The diameter of the mucilage canals in the pith is 180 to 190 μ. Their inner walls are covered with epithelial cells (Fig. 5.).

The vascular bundle ring. The vascular bundle ring is divided up by the primary pith rays, taking their origin from the pith, into more or less broad collateral vascular bundles (Fig. 1.). The xylem of the broader vascular bundles is conically tapering towards the pith in the cross section. The primary pith rays are 3 to 6 cells wide; in these the common vascular bundles of the pith and as a rule next to them the mucilage canals are running (Fig. 7.). In the primary pith rays the pith ray cells are elongated elliptic or brick shaped, their radial dimension 370 to 400 μ, their width at most 70 μ. The walls are extremely thin, not pitted at all (Fig. 4.). Some are filled out by calcium oxalate crystal druses. The cells of uniseriate pith rays are radially much shorter, their radial dimension being 50 to 100 μ, their width about the same. In some pith rays also thick-walled sclerenchyma cells are aligned, which appear to be septate fibres (Fig. 7.).

Xylem bundles. In the xylem the tracheids are in general radially arranged, their walls are of a uniform thickness (7 to 8 μ), their radial dimension 50 to 60 μ, their width about the same or somewhat more. The cell cavities (lumina) are invariably rounded off (Fig. 4.) representing circles or ellipses, while the outer walls are polygons. Radially the bordered pits are conspicuous,

while on the tangential side pits occur but exceptionally. Among the tracheids — very rarely — thin-walled wood parenchyma cells are found (Fig. 4.).

Cambium. Next to the xylem, outwards, at some places a 3 to 4-seriate cambium layer follows (Fig. 4.). The cell walls are thin and completely smooth.

Phloem bundles. Similarly to the xylem, also the phloem is divided up by primary and secundary pith rays (Fig. 4.). The structure of the pith ray cells in the phloem is analogous to those of the xylem. The phloem consists predominantly of thick — walled bast fibres (1) the lumina of which are narrow and always circular or elliptic. Sometimes the stratification of the walls can be definitely determined. Among them sporadically thin-walled parenchyma cells are found (2). In rare cases — particularly in the exterior part of the phloem — the pores of the sieve-tubes can be observed.

The normal xylem and phloem ring is followed by the second, so called abnormal xylem and phloem ring (*cd—c*), the structure of which closely corresponds to the former, with the only difference, that this second xylem layer is somewhat thinner (Fig. 1.).

Cortex The cortex consists of ground tissue cells of the same structure as that of the pith cells; both the single vascular bundles and the mucilage canals present the same structure and arrangement as was found in the pith.

Towards the exterior portion of the cortex follows a rather broad layer of sclerenchyma cells (Fig. 6.). These cells are, as a matter of fact, thick-walled idioblasts fitting loosely to each other at some places and closely at others. Sometimes they are suggestive of thick walled twin fibres. On the evidence of their cross sections two types of the sclerenchyma cells can be distinguished: the first with comparatively thin walls, while the second with quite thick walls, appearing to be typical stone cells. This sclerenchyma layer, the cells of which are more characteristic, provides for the strength of the wood. The other cells of the cortex are thinwalled and non-pitted.

The periderm. At the outermost part of the cortex the periderm cells are brick shaped, suberized, and fitting closely to each other, generally succeeding in radial rows *(f)*.

Tangential microsection. On the tangential microsection the primary pith rays have a width of 15 to 20 cell layers, while the secundary pith rays, as a rule, of 1 to 3 cells (Fig. 7.). The height of the pith ray cells ranges from 70 to 150 μ, their width from 50 to 60 μ. The walls are very thin and smooth. In some pith rays, especially at the corner cells, also thick-walled sclerenchyma cells occur, which can be easily recognized from being simply pitted (3). In the tangential wall of the tracheids bordered pits can be observed but exceptionally. In the broader pit rays it is easy to recognize the mucilage canals and vascular bundles conducting outwards from the pith (Fig. 7. 1—2). Among the thin-walled pith ray cells the thick-walled sclerenchyma fibres (3) which probably also run from the pith outwards into the cortex are rather frequent. All this is very conspicuous in Fig. 7.

Radial section. Pith rays. The pith ray cells are generally erect parallelepipeds or squares (Plate VII. Fig. 11.) of 80 to 120μ height and 60 to 70 μ

width. The walls are entirely smooth and thin. Definite crossfields can be observed but very rarely. The parenchyma cells bordering on the tracheids communicate with the longitudinal parenchyma cells mostly by scalariform perforations. The existence of scalariform perforations is confirmed by the fact that the scales at some places form larger or smaller groups (Fig. 10), while in other cases they can be observed all over the length of the tracheids (Fig. 8. 9.). When in some cross-fields pits occur, their number is 10 to 12 and they are generally arranged in 2 to 3 longitudinal rows (Fig. 11.). Often longitudinal parenchyma cells also adhere to the pith rays. The height and width of these parenchyma cells is 220 to 250 μ and 22 to 24 μ respectively.

Tracheids. The most characteristic feature of the wood is the typical araucaroid pits and scalariform thickening or scalariform perforation. (Fig. 8—12). In the broader tracheids the bordered pits are arranged in 3 to 4 rows as the compartments of a honeycomb. The apertures have the shape of small sticks never reaching the border. In other tracheids — sometimes in near proximity to the formerfrequently thickenings with scalariform perforations are seen which are likely to form only on the sides touching the pith rays; this is supported by the fact that on the other side of the tracheid the bordered pits are arranged according to the araucaroid pattern (Fig. 8—12). These scalariform perforations or thickenings are very characteristic at some places and form all over the length of the tracheids, being suggestive — strange as it may sound — of the scalariform perforations in Palms. No such scalariform perforation structure has been established yet in *Cycadales* examined hitherto; this is why the separation of *Lepidozamia* appears to be fully justified also from the anatomical point of view. These scalariform thickenings should by no means be mistaken for spiral thickenings. In the case of spiral thickening the spiral laths are equally thick over their whole length, while these scales are broadening at both ends, pointing to the origin of the scale intervals from the elongation of the bordered pits. In some broad pith ray among the thin walled pith ray cells also thick walled cells occur, in perfect agreement with the phenomena referred to at the tangential side.

Examination of the leaf epidermis. The leaf of *Macrozamia hopei* is hypostomatic, stomata occurring on the lower surface of the leaf blade only.

Upper surface of leaf blade. On the upper surface of the leaf in longitudinal direction the epidermis cells do not separate into definite longitudinal strips. In some places however from the grouping and shape of the cells it may be concluded that the epidermis cells immediately above the veins are of a different form. The epidermis cell walls are thick and generally fit to each other in a wedge pattern. They form a triangle, rhombus or a stretched quadrangle with oblique ends (see Photo). Among the thick-walled epidermis cells occasionally some thin-walled are found. The walls are not absolutely uniform in thickness, at some places they become thinner, at others thicker, so that external contours and inner walls are not quite parallel. The length of the cells varies between 190 and 200 μ, their greatest width ranging from 22 to 25 μ. The thickness of the double wall is 7 to 10 μ, but may be much more or less (ham-shape) (Plate VIII. Fig. 1. 2.).

On the **lower surface** the cells are much more variable in shape and slightly shorter in size, the thickness of the walls, however, is the same as in the cells of the upper surface. The stomata are arranged in 4 to 5 rows in longitudinal strips, somewhat irregularly. The apertures are not always parallel to the longitudinal leaf axis, but sometimes perpendicular (Fig. 4.). Their length is 35 to 36 μ and their total length including the outer wall of the guard cells about the same. Between the two thin-walled polar cells the conic apex is marked, although both ends of the guard cells have definite endings. The dimensions of the aperture are 28 to 35μ. The contact line of the two guard cells which are terminated by 6 cells is in the middle of the aperture. No cross-stripes or design is observed on the thick wall of the guard cells (Plate VIII. Fig. 3. 4.).

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Comment to the Plates

Plate I.

Fig. 1. Cross-section surface picture; *a*, pith; *b*, transfusion portion; *c*, *d*, double phloem ring; *e*, cortex; *f*, periderm; (*Cycas revoluta* 1/3×).

Fig. 2. Portion of the periderm. Calcium oxalate crystals in the dark cells (*Macrozamia macdonelli*, 50×).

Fig. 3. Mucilage canal from the cortex (*Stangeria eriopus*, 100×).

Fig. 4. Cross section structure; *a*, pith with mucilage canals; *b*, transfusion part; *c*, xylem ring; *d*, phloem ring; *e*, cortex with mucilage canals; *f*, periderm (*Zamia skinneri*, 10×).

Fig. 5. Vascular bundle; *c*, xylem; *d*, phloem, darker points representing bark fibres, thin-walled cells are phloem parenchyma and pith ray cells. Between xylem and phloem the cambium (*Cycas rumfii*, 50×).

Fig. 6. Portion of the phloem; 1. thin-walled pith ray cells; 2. thin walled phloem parenchyma cell; 3. thick-walled sclerenchyma fibre; 4. thick-walled bark fibre; 5. sieve tube (*Cycas rumfii*, 100×).

Fig. 7. Cross section of mucilage canal in the ground tissue of the pith (*Encephalartos altensteinii*, 100×).
Fig. 8. Ground tissue cells from the pith (*Stangeria eriopus*, 30×).
Fig. 9. Portion of the xylem. Among the tracheids uni- and biseriate thin-walled parenchyma cells (*Encephalartos villosus*, 100×).

Plate II.

Fig. 1. Transfusion cells before the xylem bundle (*Zamia floridiana*, 100×).
Fig. 2. Transfusion cell and calcium oxalate crystal druse (*Encephalartos barteri*, 200×).
Fig. 3. Transfusion cell with reticulate thickening (*Microcycas calocoma*, 300×).
Fig. 4. Next to the transfusion cells thin-walled parenchyma cell. The walls of the transfusion cells show bordered-pitted thickening (*Macrozamia Pauli guilielmi*, 300×).
Fig. 5. Tangential section. 1-, 2, and multiseriate pith ray structure. (*Lepidozamia hopei* 50×).
Fig. 6. Thich-waled idioblasts and stone cells from the cortex. (*Lepidozamia hopei* 300×).
Fig. 7. Tangential section. Pith ray structure from the phloem (*Macrozamia douglasii*, 100×).
Fig. 8. Pith ray structure from the xylem. Tiny bordered pits in the tangential wall of the tracheids (*Macrozamia douglasii*, 100×).
Fig. 9. Pith ray structure. Araucaroid bordered pits on the tangential wall (*Macrozamia miquellii*, 100×).

Plate III.

Fig. 1. Radial sections. In the radial wall of the tracheids the bordered pits are arranged according to the araucaroid pattern (*Encephalartos gratus*, 300×).
Fig. 2. In the radial wall of the tracheids the bordered pits are arranged according to the araucaroid pattern; on one side of the tracheid scalariform thickening, possibly perforation (*Lepidozamia hopei*, 300×).
Fig. 3. In the radial wall of the tracheids the bordered pits are arranged loosely, still according to the araucaroid pattern; the aperture is crossed, on the right side of the picture scalariform thickening, possibly perforation (*Cycas media*, 300×).
Fig. 4. Various thickenings in tracheids. Ring-shaped, spiral and scalariform thickening (*Dioon edule*, 300×).
Fig. 5. Loose scalariform thickening in the walls of tracheids (*Zamia furfuracea*, 300×).
Fig. 6. Loose scalariform thickening in the walls of tracheids (*Encephalartos barteri*, 300×).
Fig. 7. Cross-fields from the pith rays of *Encephalartos gratus*. 18 pits irregularly arranged in one cross-field (300×).
Fig. 8. No cross-fields are seen in *Microcycas;* the pith ray walls are absolutely smoth and thin (300×).
Fig. 9. Various kinds of cell wall thickenings in the tracheids. At the left side of the picture the transversal septum between two tracheids (*Zamia skinneri*, 200×).

Plates IV—V.

Microcycas calocoma

Fig. 1. Cross section surface picture; *a*, pith; *c*, *d*, xylem and phloem ring; *e*, cortex; *f*, periderm (natural size).
Fig. 2. Portion from the xylem and phloem rings; *c*, xylem; *d*, phloem.
Fig. 3. Cross section structure from pith to periderm; *a*, pith with mucilage canals; *b*, site of transfusion cells; *c*, xylem bundles; *d*, phloem bundle ring; *e*, cortex with winding mucilage canals; *f*, periderm (8×).
Fig. 4. Portion of phloem bundle (100×). The thick-walled bark fibres are arranged loosely among the broad pith rays.
Fig. 5. Portion of the xylem bundle ring. Broad primary pith ray between two tracheid bundles. At the endings a few cambium cells, above these a small portion of the
Fig. 6 and 7. Reticularly thickened transfusion cells (300×).
phloem bundle (100×).
Fig. 8. Tangential section. Pith ray structure from the tangential side. Between the pith ray cells tracheids with scalariform thickenings (100×).
Fig. 9. Radial section. The wall of the pith ray cells adhering to the longitudinal tracheids is absolutely smooth and thin, no cross-fields are observed (300×).

Fig. 10. Tracheid with scalariform thickening. Radial side (300×).
Fig. 11. In the tracheid walls the bordered pits are arranged according to the araucaroid pattern and forming a transition to the scalariform thickening (300×).
Fig. 12. Arrangement of the bordered pits, various elongation and shape of their apertures in the radial tracheid walls. Transition to the scalariform thickening (600×)

Plates VI—VII.

Lepidozamia hopei

Fig. 1. Cross section and surface picture, natural size; *a*, pith; *c*, *d*, xylem and phloem rings; *e*, cortex; *f*, periderm.
Fig. 2. Cross-section structure (7×): *a*, pith; in the ground tissue the pith bundles (black) and mucilage canals (white);*c*—*c*, xylem; *d*—*d*, phloem.
Fig. 3. The meeting of xylem and phloem. The bulk of the phloem consists of thick-walled bark fibres; *c*, xylem; *d*, phloem. (30×).
Fig. 4. The same enlarged 100×; *c*, xylem, above: cambium, over this: phloem *(d)*. In the phloem thick-walled bark fibres (1), among them wood parenchyma cells (2). 1- and 3-seriate pith rays *(r)*.
Fig. 5. Cross section of mucilage canal from the pith. Similar canals are in the cortex.
Fig. 6. Thick-walled idioblasts and stone cells from the cortex.
Fig. 7. Tangential section. 1-, 2- and multiseriate pith ray structure. At the base of the primary broad pith ray mucilage canal (1). To the right: cross section of common xylem bundle (2). To the left from this: some thick-walled parenchyma cells (50×).
Fig. 8. Araucaroid pits of three tracheids; in the middle one scalariform perforation (300×).
Fig. 9. The same. In the two right side tracheids scalariform perforation, the wall behind pitted in the araucaroid pattern (300×).
Fig. 10. In the right side tracheid definite scalariform perforation (300×).
Fig. 11. Meeting of pith ray cells and longitudinal tracheids. In the two right side tracheids scalariform perforation (300×).
Fig. 12. In the left side tracheid araucaroid pit, in the side scalariform perforation. Behind the perforation araucaroid pits (600×).

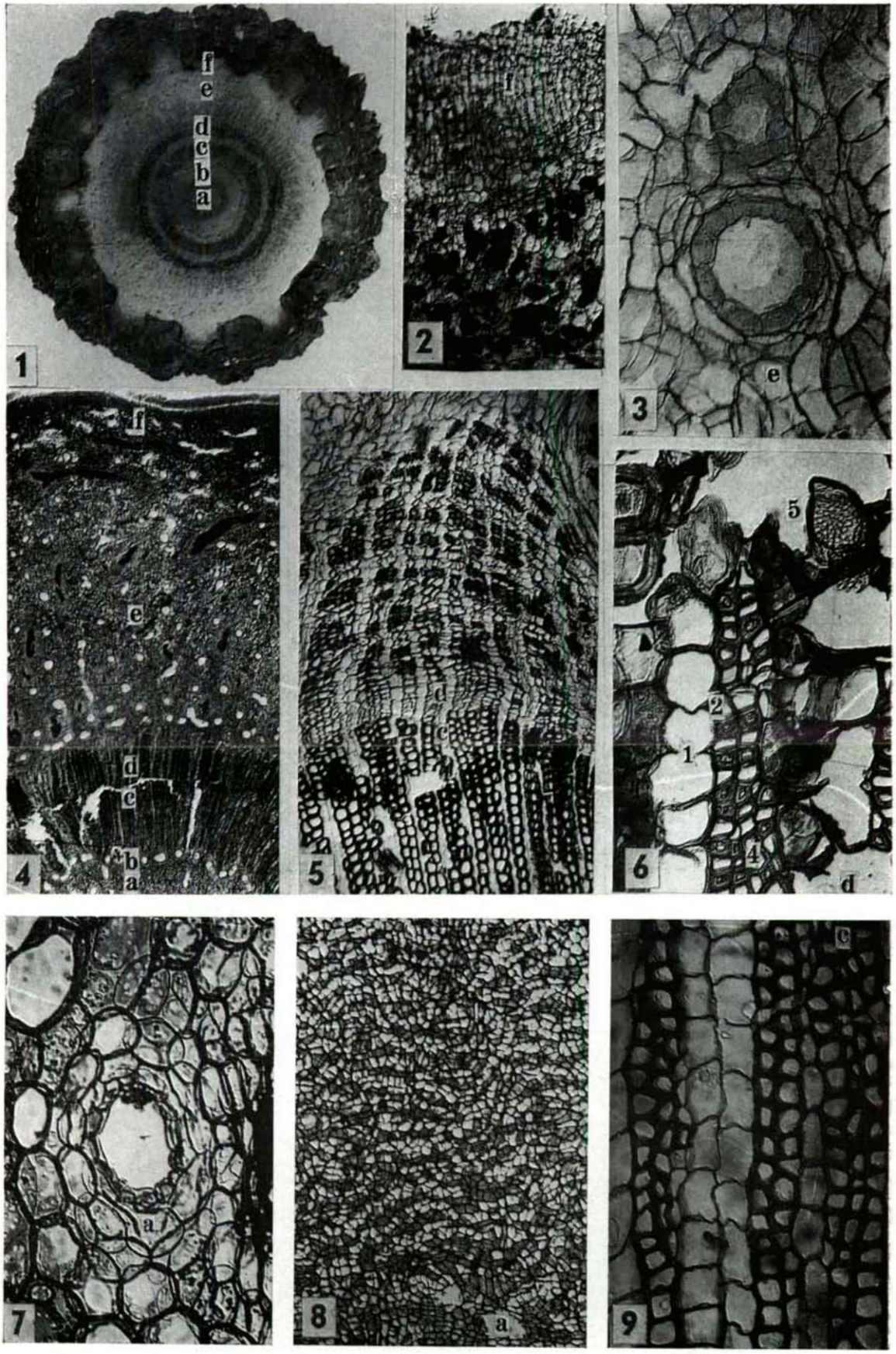
Plate VIII.

Microcycas calocoma

Fig. 1. Upper epidermis structure (50×).
Fig. 2. The same (300×).
Fig. 3. Lower surface of the leaf blade. The stomata are arranged in longitudinal strips (50×).
Fig. 4. The structure of two stomata (300×).

Lepidozamia hopei

Fig. 1. Upper epidermis structure (50×).
Fig. 2. The same (300×).
Fig. 3. Lower surface of the leaf blade. The stomata are arranged in longitudinal strips (50×).
Fig. 4. The structures of four stomata (300×).



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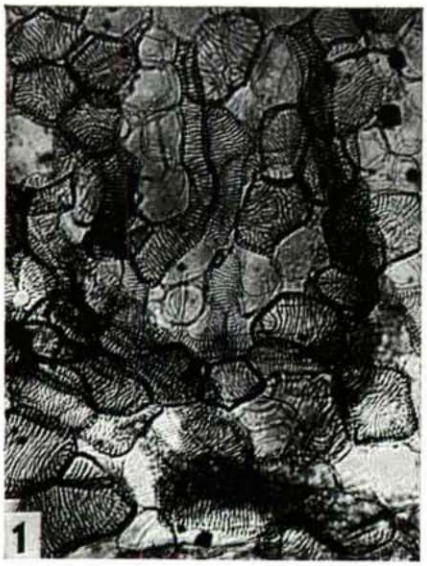

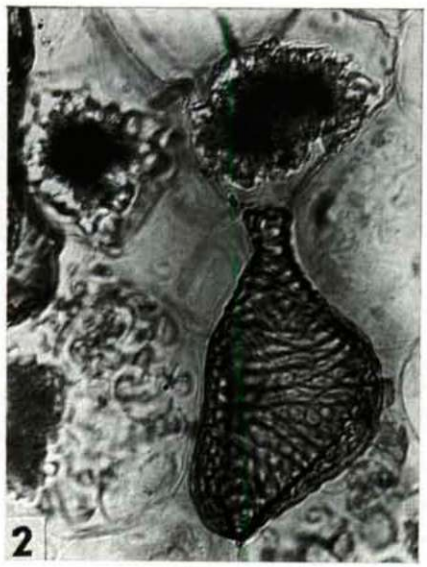

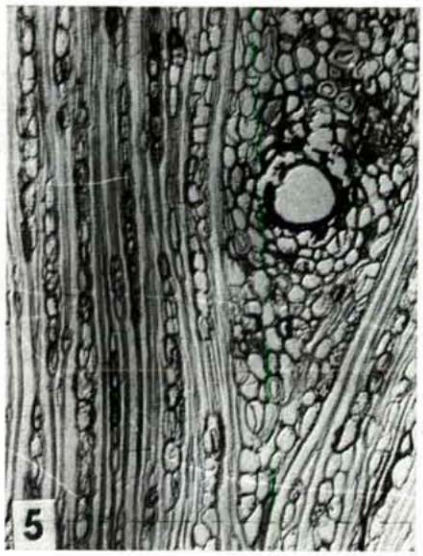

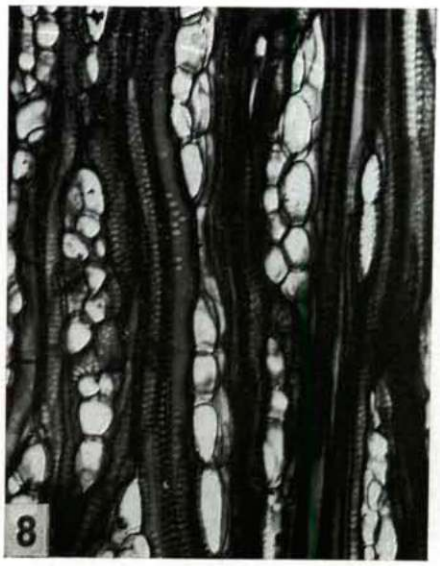

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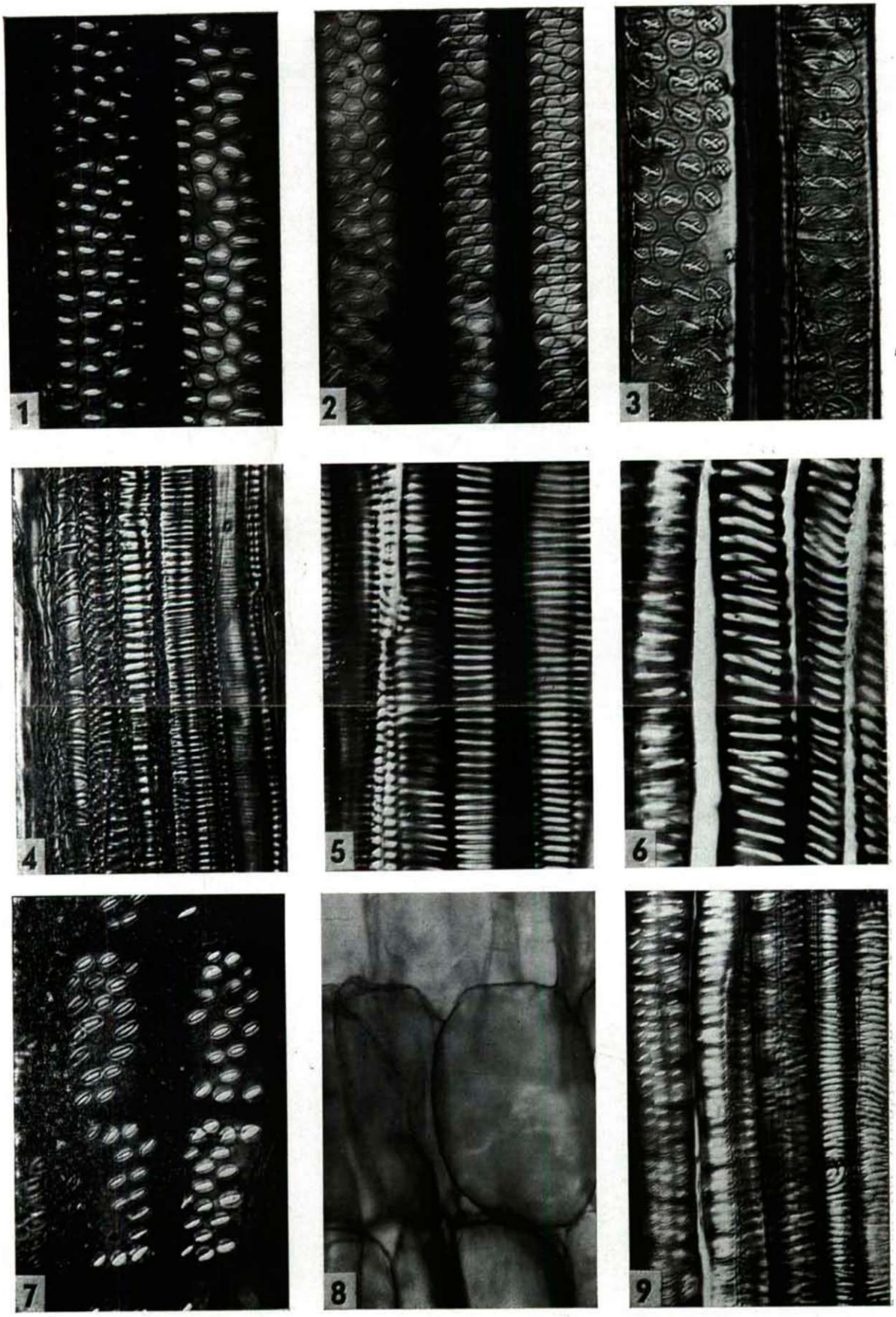

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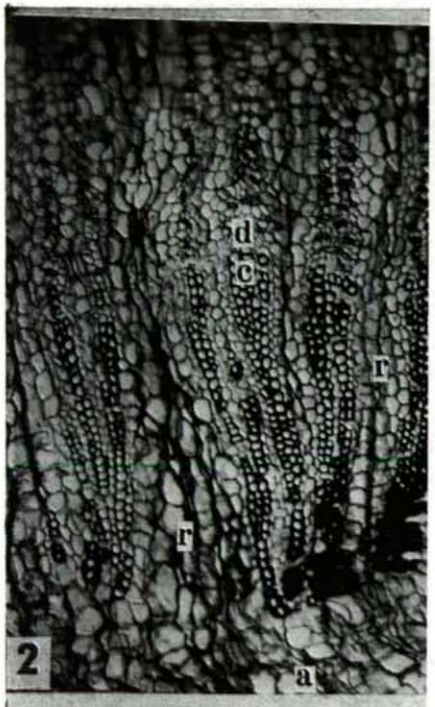

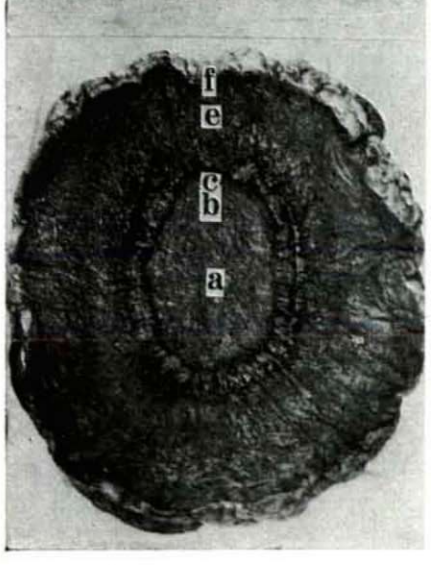

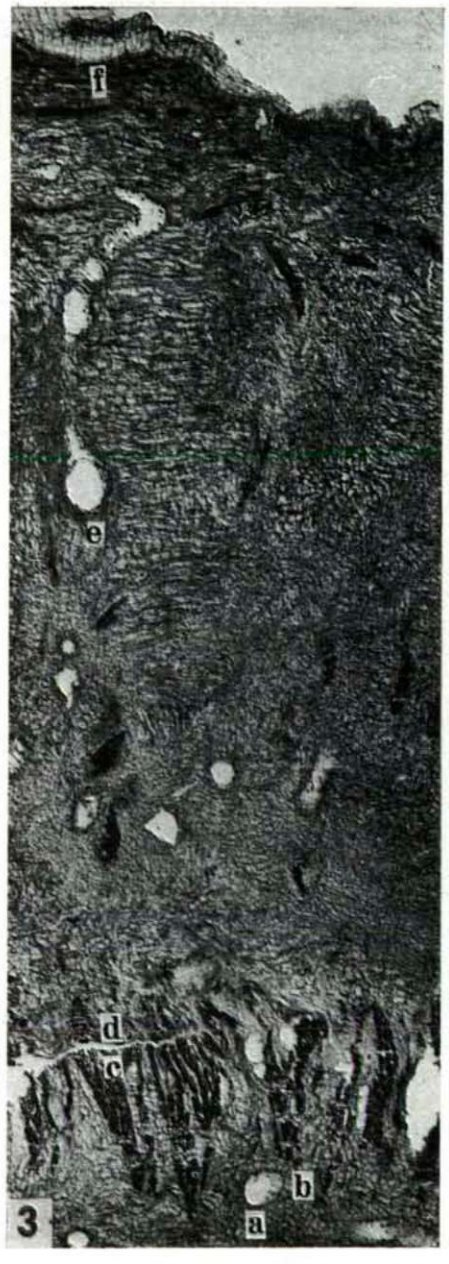

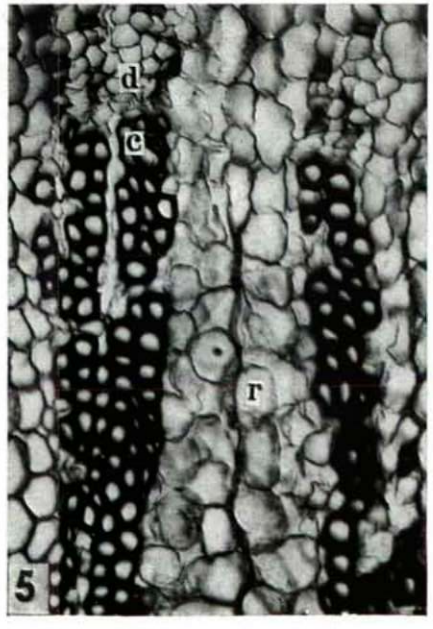

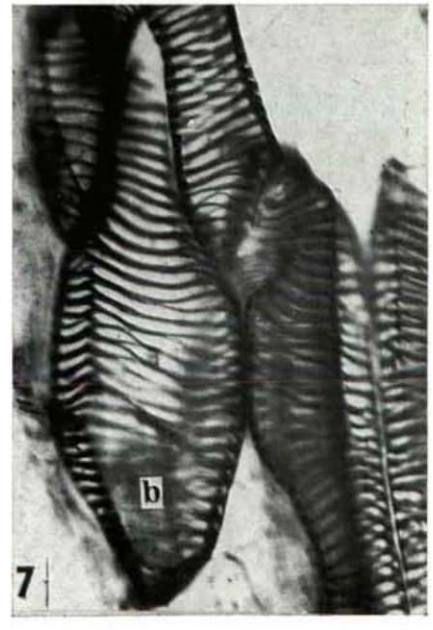

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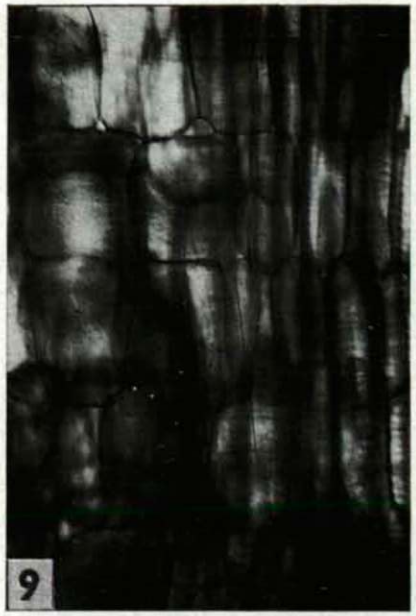

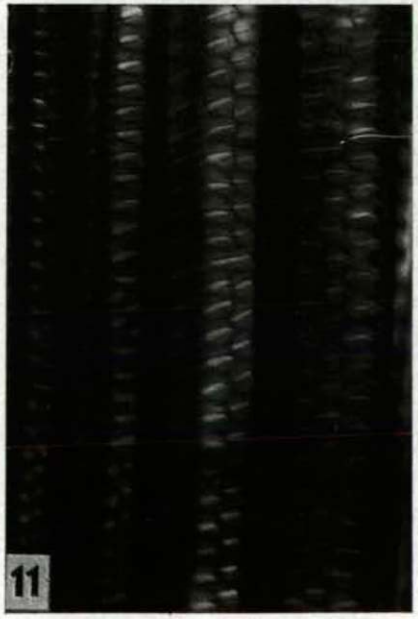

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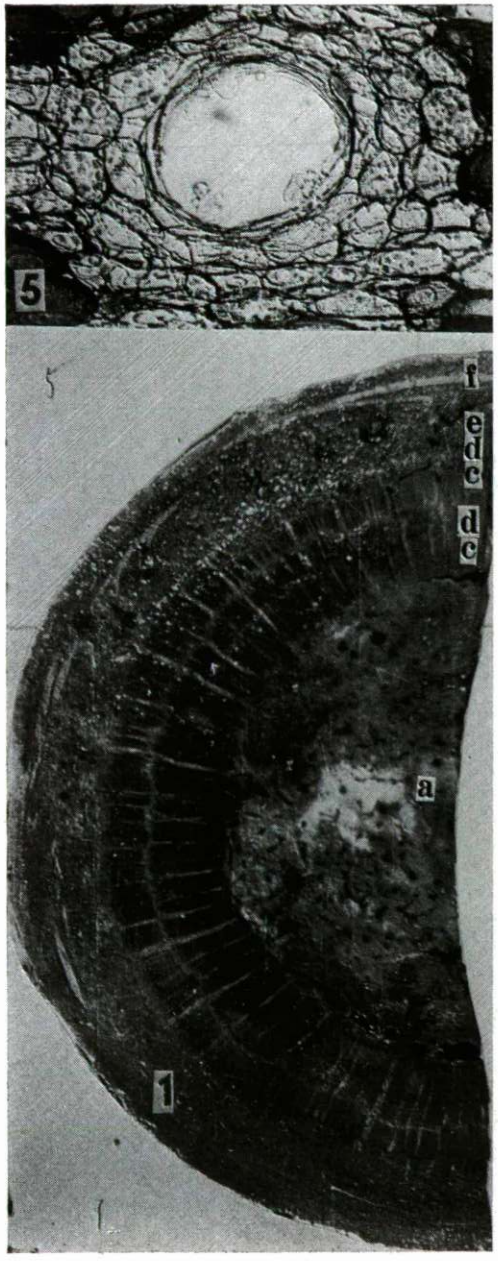

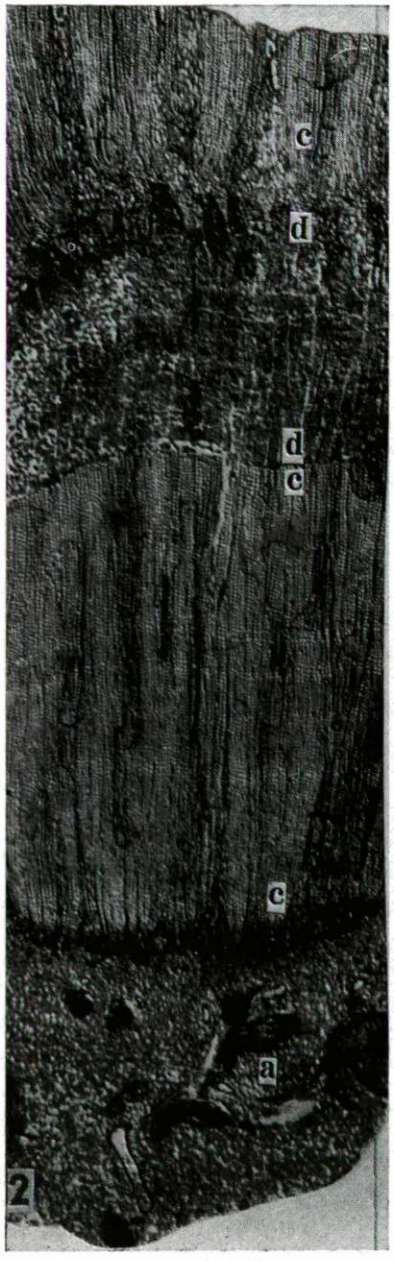

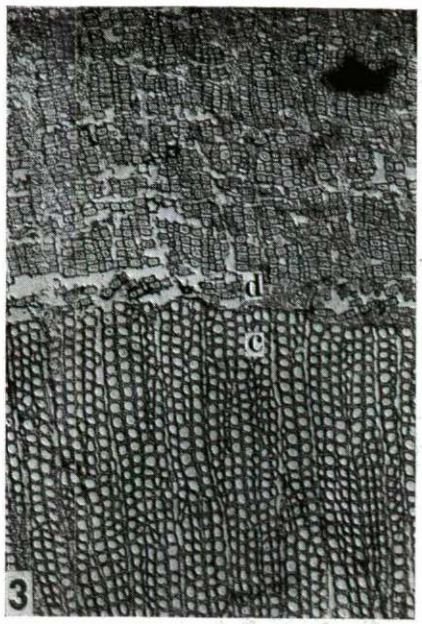

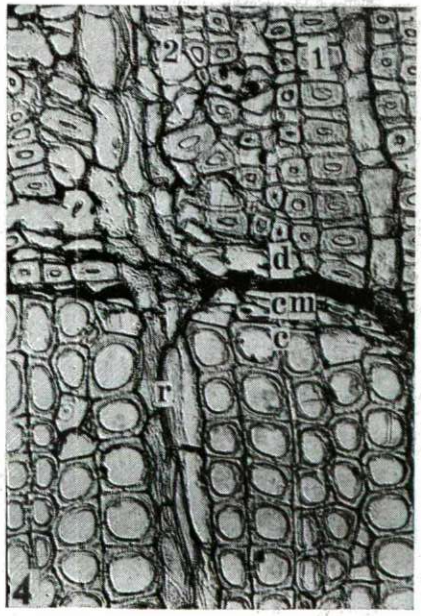

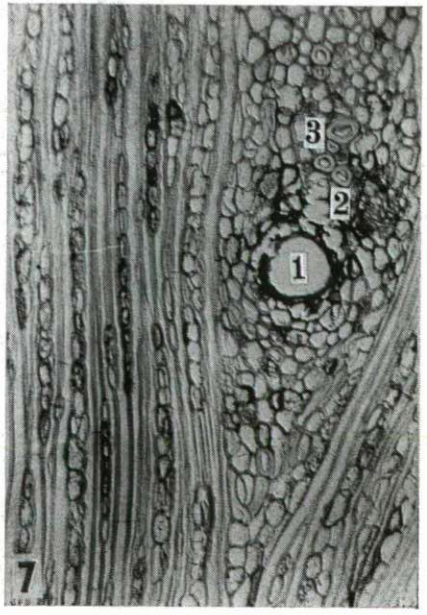

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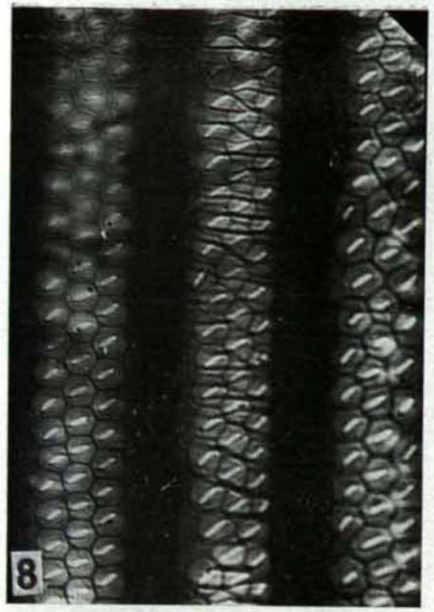
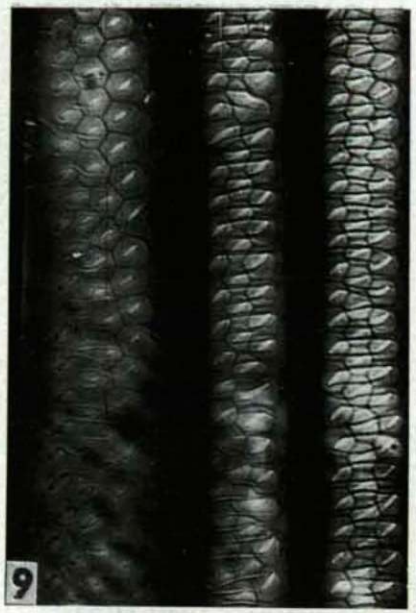
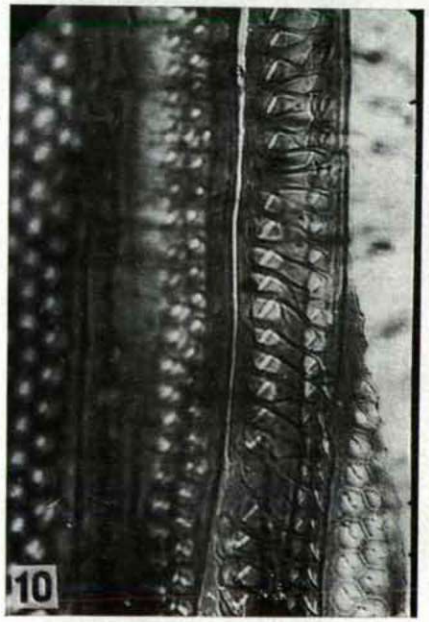
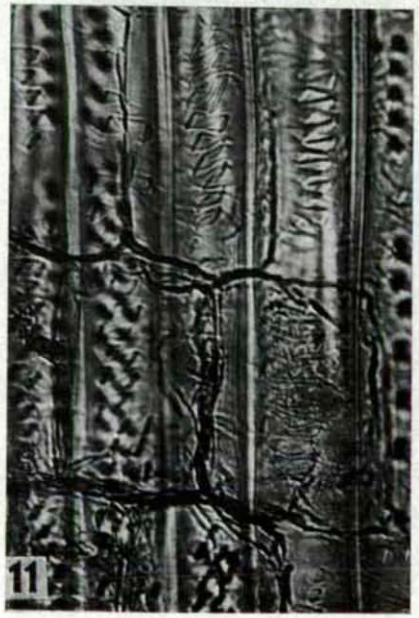
Lepidozamia hopei Regel









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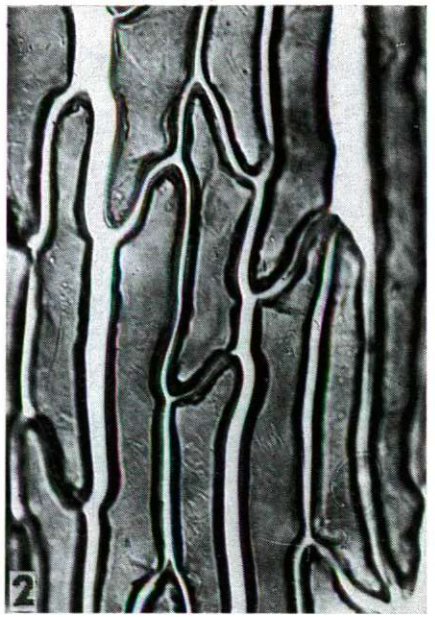
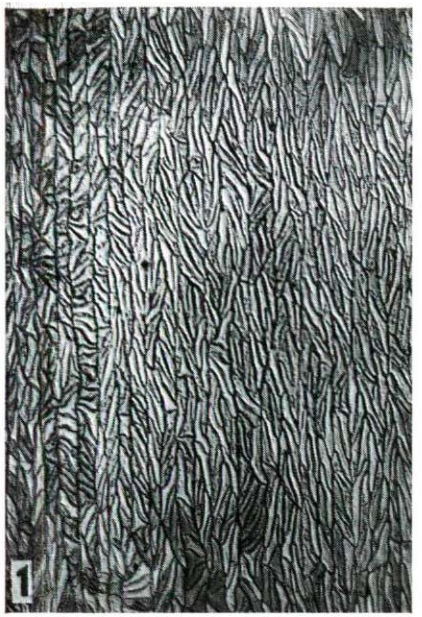
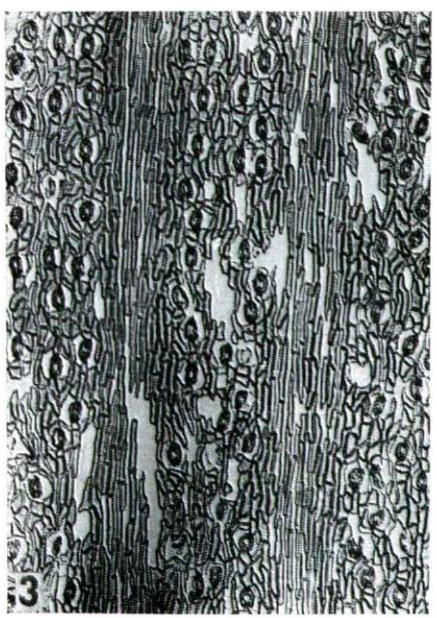
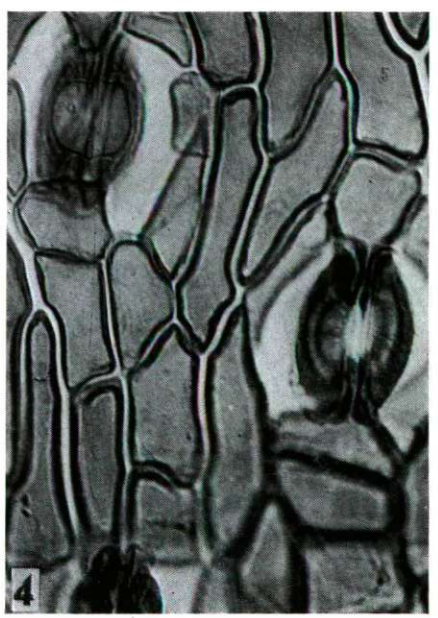
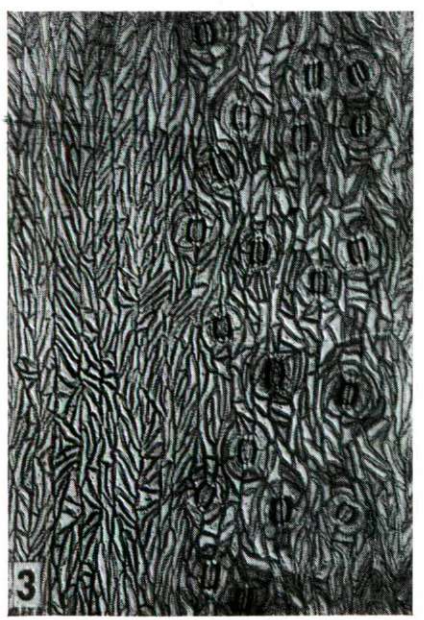
Lepidozamia hopei Regel











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Microcycas calocoma (Mig.) A. DC.

Lepidozamia hopei Regel